Migratory bats are sensitive to magnetic inclination changes during the compass calibration period

Schneider, William T; Holland, Richard A; Keišs, Oskars; Lindecke, Oliver

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William T. Schneider[1,a], Richard A. Holland[1], Oskars Keišs[2], Oliver Lindecke[1,3,a]

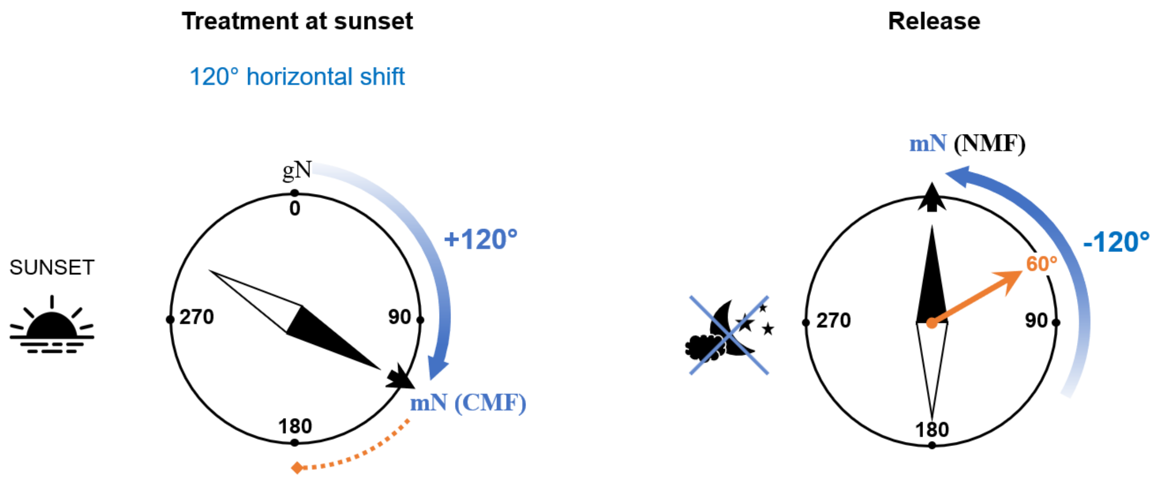
[1] School of Natural Sciences, Bangor University; Bangor, Gwynedd LL57 2UW, UK; email: w.schneider@bangor.ac.uk

[2] Laboratory of Ornithology, Institute of Biology, University of Latvia; Rīga LV–1004, Latvia.

[3] Institute for Biology, Carl-von-Ossietzky Universität Oldenburg; 26111 Oldenburg, Germany; email: oliver.lindecke@uni-oldenburg.de

Electronic supplementary material 1

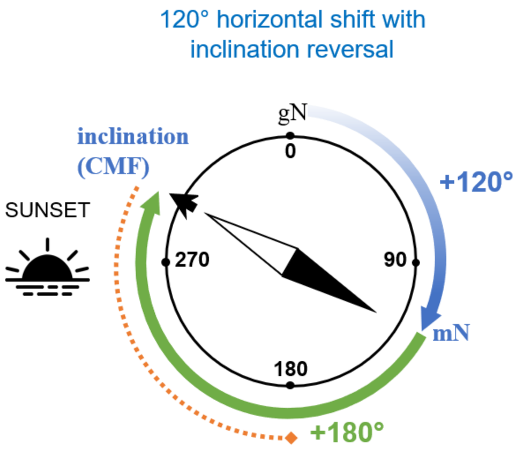
Figure S1. Predictions for orientation behaviour of bats after magnetic treatment at sunset if they calibrate a magnetic compass by sunset cues. *(a)* Magnetic treatment utilising the local characteristic inclination angle at the coastal dunes in Pape, Latvia. *(b)* The predicted bat behaviour after the treatment for southwards migrating Soprano pipistrelle bats.



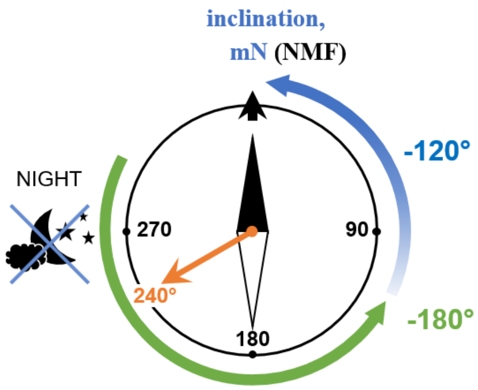
Bats exposed to a changed magnetic north (CMF) at sunset experience magnetic North (mN) +120° relative to geographical North (black part of compass needle indicates the polarity of the magnetic field, blue arrow shows the degree of shift in the declination of the field). Bats intending to fly southwards later at night will perceive their goal to be 60° clockwise of mN (orange diamond) if the sunset calibrates the magnetic field.

If they have calibrated the magnetic compass to the sunset, when released in the natural magnetic field (NMF) bats aiming for take-off in a southerly direction will now perceive mN in its natural direction. To fly in their goal direction, they would be expected to fly 60° clockwise of mN. Take-off would thus be predicted to be at the 60° compass direction for a sunset calibrated magnetic compass (orange arrow).

Figure S2. Prediction for the orientation behaviour of bats depending on whether the magnetic compass is inclination or polarity based. *(a)* Magnetic treatment utilising the reversed local characteristic inclination angle at the coastal dunes in Pape, Latvia. *(b)*The predicted bat behaviour after the treatment for southwards migrating Soprano pipistrelle bats



Bats exposed to a magnetic field shifted +120° (blue arrow) and magnetic inclination reversed (green arrow) at sunset experience geographical North (gN) +60° relative to magnetic North (mN) of the CMF if their compass is based on inclination of the magnetic field (120° declination + 180° inclination reversal=300° for CMF). Inclination compasses indicate the polewards direction as inclination increases relative to the Earth's surface. Bats intending to fly southwards later at night perceive their goal to be 120° counter-clockwise from mN (orange diamond).



If they have calibrated an inclination based magnetic compass to the sunset, when released in the natural magnetic field (NMF) bats aiming for take-off in a southerly direction will perceive mN and inclination in its natural direction and angle. To fly in their goal direction, they would be expected to fly 120° counter clockwise of mN and the inclination angle. Take-off would thus be predicted to be at the 240° compass direction for a sunset calibrated magnetic compass (orange arrow). If the compass is not inclination based, the predictions for this manipulation would be expected to be as figure S1 as only the polarity of the field, not the inclination reversal will have been considered.

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[2] Laboratory of Ornithology, Institute of Biology, University of Latvia; Rīga LV–1004, Latvia.

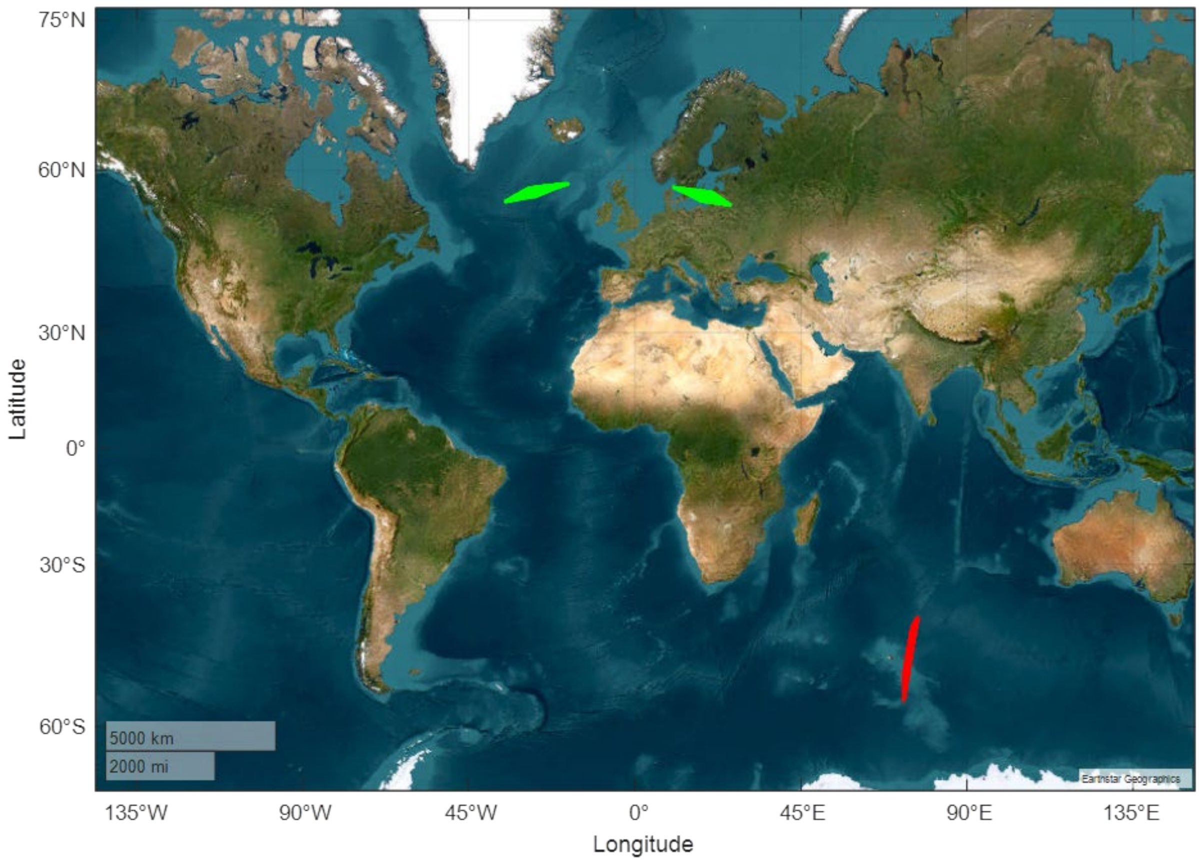
[3] Institute for Biology, Carl-von-Ossietzky Universität Oldenburg; 26111 Oldenburg, Germany; email: oliver.lindecke@uni-oldenburg.de

Electronic supplementary material 2

Magnetic locations on Earth that share the field conditions created by both experiments during sunset compass calibration

We applied the visualisation tool for possible locations of virtual magnetic displacements (ViMDAL) to evaluate which locations on Earth share the magnetic parameters set in the magnetic coil during our treatments [1], a shift of the magnetic North by 120° and a 120° shift plus reversal of magnetic field inclination.

Figure S3. Magnetic locations on Earth that share similar magnetic field conditions as created inside the magnetic coil during sunset. Green are the possible locations for the 120° shift experiment, red are possible locations for the experiment involving a 120° shift plus the inclination reversal. In both cases, total intensity varies by +/- 250 nT, inclination by +/- 0.5 degrees. Note, the locations (green) in the North Atlantic, as well as the locations simulated by the inclination reversal (red) which are found in the Indian Ocean are outside of the distribution range of *Pipistrellus pygmaeus* which is a western Palearctic species occurring on the European continent with its range extending from Asia Minor to northern Norway [2].



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[2] Laboratory of Ornithology, Institute of Biology, University of Latvia; Rīga LV–1004, Latvia.

3 Institute for Biology, Carl-von-Ossietzky Universität Oldenburg; 26111 Oldenburg, Germany; email: oliver.lindecke@uni-oldenburg.de

Electronic supplementary material 3

Likelihood-based modelling approach to evaluate circular data distributions of non-unimodally oriented test groups.

Table S1. Model-based analysis of nightly bat take-off orientations. Selections for the best models to describe the data are made using the guide of *Fitak & Johnsen* [1].

	Control		Shift minus	
Model	ΔAICc	*w*	ΔAICc	*w*
M1 (uniform)	4.30	0.06	**0.00***	**0.67***
M2A (unimodal)	8.83	0.01	6.18	0.07
M2B (symmetric modified unimodal)	8.00	0.01	6.16	0.07
M2C (modified unimodal)	7.02	0.01	9.76	0.02
M3A (homogenous symmetric bimodal)	0.00	0.00	5.59	0.10
M3B (symmetric bimodal)	2.56	0.14	8.64	0.03
M4A (homogenous axial bimodal)	**2.12***	**0.17***	8.59	0.03
M4B (axial bimodal)	4.84	0.04	11.69	0.01
M5A (homogenous bimodal)	4.70	0.05	11.76	0.01
M5B (bimodal)	7.23	0.01	14.87	0.00

w = AICc model weights * Best model to describe the distribution.

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Mardia-Watson-Wheeler (MWW) tests.

Table S2. Comparison matrix providing results from MWW tests for all test groups. W-scores (W) in the lower half and probabilities (p) in the upper half.

	Controls	120° shift mN	120° shift mN & inclination reversal
Controls	-----	0.638	0.81
120° shift mN	*0.9*	-----	0.039
120° shift mN & inclination reversal	*0.421*	*6.511*	-----

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Electronic supplementary material 4

To test whether the coil, or specifically the vertical axis of the coil, was producing RF noise that may differ between the treatments in our experiment we used a single wrapped Helmholtz coil (the same model used in the experiments in Latvia) and a passive antenna placed either vertically (Figure S4) or horizontally (Figure S5) connected to a spectrum analyser (MP700022 EU-UK). The coil was either unpowered (black trace), turned on with the power settings matched to those used in the 120 degree shift positive inclination treatment used in our experiment (red trace), or turned on with the power matched to the negative inclination treatment. The spectrum analyser was set to record ‘Max Hold’ – collected the maximum power readings at all frequency bands during a 30 second window.

Whist there was clearly the presence of background RF signals (e.g. the 100 MHz spike can be attributed to FM radio signals), these were present at the same level in each of the recordings we took, with no differences that may suggest RF noise produced by the coil may have caused the differences that we observed in our treatments.

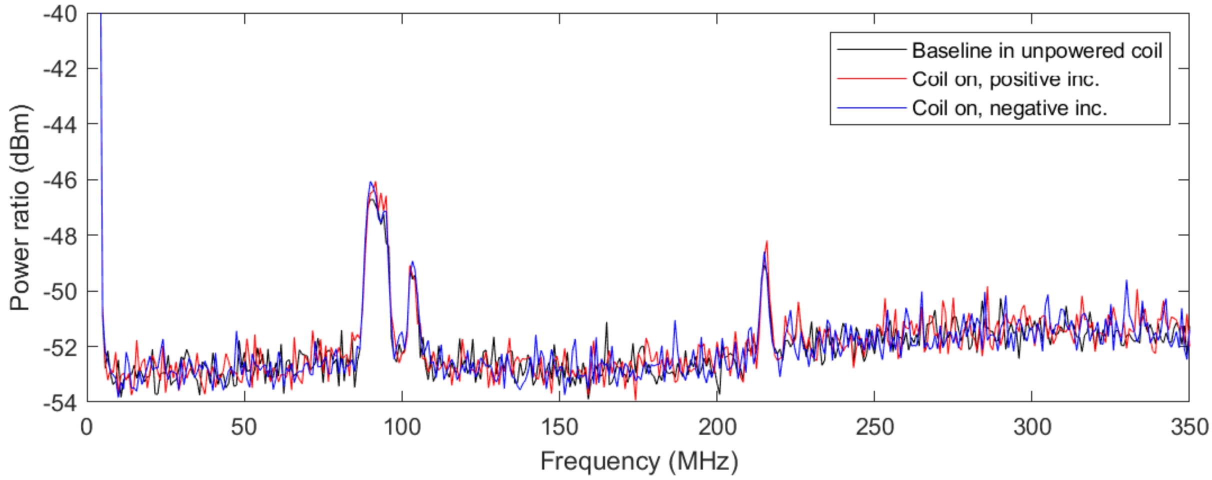

Figure S4. RF power spectrum with antenna mounted vertically.

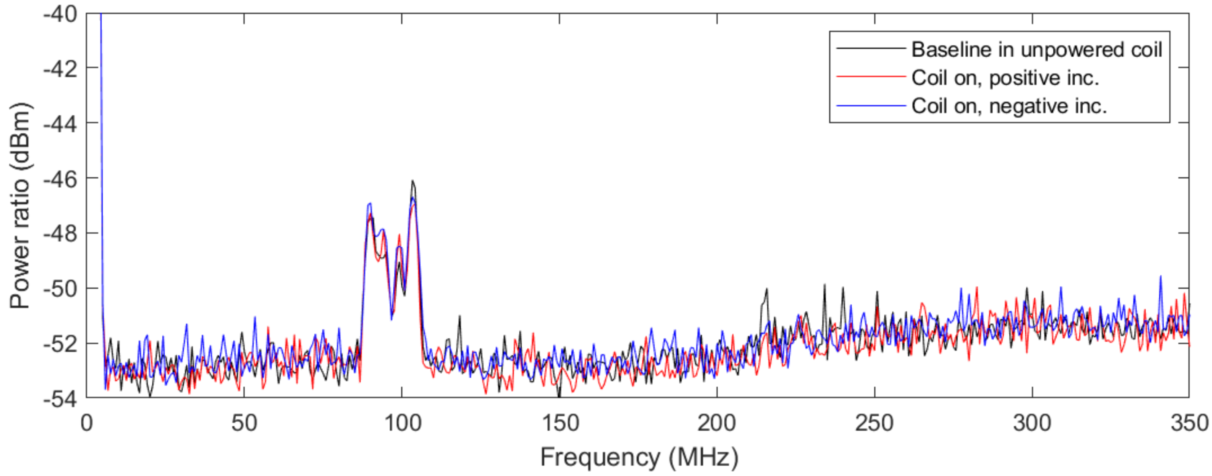

Figure S5. RF power spectrum with antenna mounted horizontally.

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[1] School of Natural Sciences, Bangor University; Bangor, Gwynedd LL57 2UW, UK.
[2] Laboratory of Ornithology, Institute of Biology, University of Latvia; Rīga LV–1004, Latvia.
[3] Institute for Biology, Carl-von-Ossietzky Universität Oldenburg; 26111 Oldenburg, Germany.
[a] Authors for correspondence. E-mail: w.schneider@bangor.ac.uk; oliver.lindecke@uni-oldenburg.de

W.T. Schneider orcid.org/0000-0002-5197-5436

R.A. Holland orcid.org/0000-0003-4495-8061

Oskars Keišs orcid.org/0000-0001-7206-1003

Oliver Lindecke orcid.org/0000-0002-2545-9999

ABSTRACT

The Earth's magnetic field is used as a navigational cue by many animals. For mammals, however, there is little data to show that navigation ability relies on sensing the natural magnetic field. In migratory bats, however, the calibration of a magnetic compass became plausible following experiments demonstrating a role for the solar azimuth at sunset in their orientation system. Here, we investigated how an altered magnetic field at sunset changes the nocturnal orientation of the bat *Pipistrellus pygmaeus*. We exposed bats to either the natural magnetic field, a horizontally shifted field (120°), or the same shifted field combined with a reversal of the natural value of inclination (70° to -70°). We later released the bats and found that the take-off orientation differed among all treatments. Bats that were exposed to the 120° shift were unimodally oriented northwards, in contrast to controls which exhibited a bimodal North-South distribution. Surprisingly, the orientation of bats exposed to both a 120°-shift and reverse inclination was indistinguishable from a uniform distribution. These results provide the missing link that these migratory bats calibrate a magnetic compass at sunset, and for the first time, they show that bats are sensitive to the angle of magnetic inclination.

KEYWORDS

animal navigation, magnetoreception, sunset calibration, bats, animal migration, orientation

BACKGROUND

The question of how animals navigate as they migrate vast distances over varied terrain with ever-changing cue availability has interested scientists for centuries [1]. For migratory mammals the answers to this question are largely unknown. Long distance navigation appears even more remarkable for nocturnal migrants, which must find their way without the visual landmarks that are present during daytime [2]. This is the case for many migratory bats which travel hundreds of kilometres across Europe each year [3,4]. Whilst bats do possess the ability to echolocate, it is not suitable over distances greater than tens of metres [5], therefore it seems that further navigation tools must be necessary to successfully migrate. Night migrating birds are known to use the Earth's magnetic field to aid their migratory navigation [6], but there has been no comprehensive evidence to show that migratory bats perceive the Earth's magnetic field and use it in their navigation system.

The soprano pipistrelle (*Pipistrellus pygmaeus*), is thought to migrate between north-east and south-west Europe [7]. In late summer they can be caught in great numbers on the Baltic coastline. Experimental releases of these bats have shown their take-off orientation can be measured to learn about their intended departure flight orientation [8]. Recently, it was found that adult soprano pipistrelles may calibrate compass information from the horizontal location, i.e., the azimuth of the setting sun [9], the first clear demonstration of such a mechanism to exist in animals. Earlier works in two non-migratory species of bats, *Eptesicus fuscus* and *Myotis myotis*, indicate that these animals relied on a magnetic compass to return to their home roosts at night [10,11]. However, it is not yet known for any species of migratory mammals whether a magnetic compass aids their long-distance navigation. Nevertheless, it is plausible that it is the Earth's magnetic field which derives that compass calibrated in migratory pipistrelles. Therefore, in this study, we manipulated the magnetic field around bats during their sunset calibration to investigate whether this modified their take-off orientation when they were released later at night. The treatments involved a magnetic shift of the horizontal field component, as well as a combination of the shift and a reversal of the local magnetic field inclination (detailed predictions outlined in ESM1). If their nightly take-off orientation differed when shifts in the magnetic field were applied hours before, it would suggest that the Earth's magnetic field is used in their sunset compass calibration.

METHODS

Experimental animals

Between the 20th of August 2021 and the 10th September, soprano pipistrelles (*Pipistrellus pygmaeus*) were caught at Pape Ornithological station, Latvia, using a large funnel trap [12]. Both males and females were caught as they appeared in the trap. The same night, the bats were checked for health and physical condition, aged, and then sorted by sex before being kept in darkness in wooden boxes for the calibration and release experiment the following night.

Sunset exposure

On the night of the experimental release, kept bats were individually bagged to ensure darkness until the time of sunset exposure. The sex of bats was balanced for each treatment. Half an hour prior to sunset, bats were brought to the exposure sites and placed inside the sunset calibration cages [9]. These were put on a table 50 cm off the ground and oriented towards sunset (μ_{sun} = 286°WNW). There were two exposure sites (figure 1*a*), one for control bats experiencing the natural magnetic field, and another for magnetically treated bats. The sites were approx. 100 m apart on dunes on the coast of the Baltic Sea, at Pape Ornithological station. The sites were not in view of each other due to the vegetation. Half an hour after sunset bats were returned to bags and carried to a room to be given ID's (to which the experimenter was blind), and then individually bagged again.

Magnetic treatment

During sunset exposure control animals experienced the natural magnetic field of Pape Ornithological station (51.6 latitude, 21 longitude). The magnetic field parameters for August 2021 given by the International Geomagnetic Reference Field (IGRF) 13th generation for this location are: H = 16728 nT, Z = 48432 nT, F = 51239 nT, I = 70.9°, and D = 7.3°. Manual measurements of the natural magnetic total intensity and inclination were made before every experiment using a 3 Axis Milligauss Meter (Model MR3, Alpha Lab, Inc.) magnetometer, the mean and standard deviation of these were: F = 51126 nT ± 71, I = 71.17° ± 0.48. Manipulations to the magnetic field for the magnetically treated bats were made using a single-wrapped, three-axis Helmholtz coil (Claricent, Munich; 1% homogeneity in a 60 cm diameter). One magnetic treatment was conducted at a time, with control bats being tested simultaneously on the same night. Once completed, the next magnetic manipulation experiment began, with continued testing of control bats. For the inclination experiment, bats were placed within a magnetic field shifted clockwise horizontally 120° during sunset calibration. All other magnetic parameters were kept constant. Across 8 experimental nights, the mean and standard deviation of magnetic total intensity and inclination inside the coil were: 51105 nT ± 88 and 71.05° ± 0.37. For the shift and inclination reverse experiment, bats were again placed within a magnetic field shifted clockwise horizontally 120°, and this time the Z component of the field was reversed, producing a negative inclination. This experiment lasted 4 nights, across which the mean and standard deviation of magnetic total intensity and inclination inside the coil were: 51138 nT ± 125 and -70.9° ± 0.08. Magnetic locations on Earth that share the conditions created by both experiments can be found in the electronic supplement (ESM2).

Yurt release

After the blinding procedure, individually bagged bats were placed inside a thermally lined box with a hot water bottle to prevent torpor. Releases were conducted inside a Mongolian yurt, also on the Pape Ornithological station site. The yurt was circular, 5.6m in diameter, with a height of 2.4 m at the centre and 1.5 m at the edge. In the centre of the yurt a circular release box for bats, an assay that measures take-off orientations [9], was used to conduct the releases. The experimenter outside the yurt released bat individually using a string pulley system. Upon release, a narrowband ultrasound detector (Pettersson D-100) was used to listen for any echolocation that signified take-off. Bats were given 3 minutes to take-off. Once this time had elapsed, or when a take-off had been audibly detected, the experimenter entered the yurt, the bat was re-caught, and the orientation of its take-off was recorded. Bats were then released into the wild.

Statistical methods

Mean bearings and vector lengths were calculated using Oriana 4.02 (Kovach Computing Services). The Rayleigh test was used to test for unimodal non-uniformity of circular distributions. The test suggested a non-unimodal distribution in both the control and the inclination group. To specifically describe the patterns of orientation in these groups, we followed a likelihood-based modelling approach (package CircMLE, R version 3.5.2) which allows comparison of circular data with multiple potential models of orientation [13,14]. For each experimental group, resulting models were then compared by means of the corrected Akaike information criterion (AICc) and the corresponding model weights (see the electronic supplementary material for details, ESM3). The Mardia-Watson-Wheeler (MWW) test was applied to test for significant differences among group orientations (see also, ESM3). .

RESULTS

The orientation of control bats, who experienced the natural magnetic field during sunset calibration, was homogeneously axially bimodal Northwards and Southwards (figure 1*b*), $p = 0.01$ (Rayleigh's test: $n = 26$, $Z = 4.458$, mean vector $\mu_{axial} = 9.1°$, $r = 0.4140.398$; see the electronic supplementary material, ESM2, for details of the likelihood-based modelling approach). Bats which experienced a field shifted 120° clockwise during sunset calibration had take-off orientations towards NNW ($\mu = 342.3°$), $p = 0.01$ ($n = 15$, $Z = 4.382$, $r = 0.54$). Finally, bats which were given a 120° shifted field as well as a reversed inclination (-70.9°), did not show any clear orientation at take-off, and were indistinguishable from a uniform distribution ($p = 0.917$, $n = 24$, $Z = 0.089$, $\mu = 66.9°$, $r = 0.061$; see also ESM3). This group was significantly different from the orientation of the group that was exposed to the horizontally shifted field (+70.9° inclination), $p = 0.039$ (MWW test, $W = 6.511$).

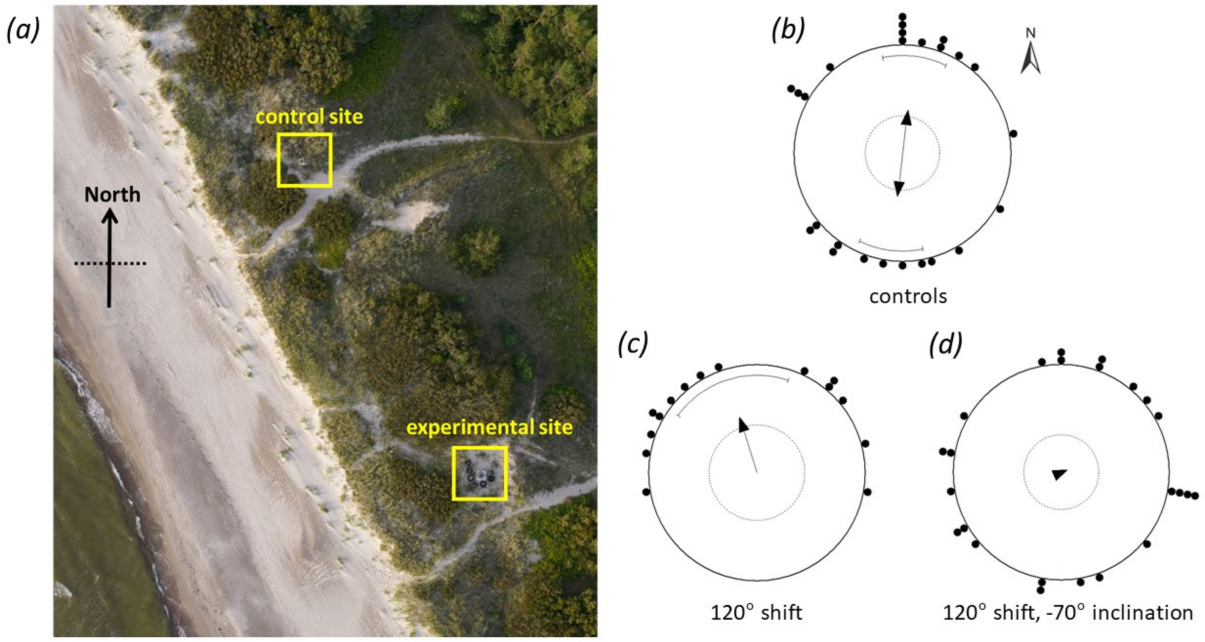

Figure 1. Sunset calibration sites (a) for control bats which experienced the natural magnetic field, and for experimental bats which experienced manipulated magnetic field conditions within a Helmholtz coil. Nightly take-off orientations under laboratory conditions on site for control bats (b), 120° horizontally shifted bats (c), and bats who experienced the horizontal 120° shift combined with a reversed magnetic inclination of -70° (d).

DISCUSSION

We found that two different manipulations of the Earth's magnetic field during sunset differentially effect the take-off orientation of migratory bats released later at night. Because the control bats flew bimodally North and South, it is difficult to assess if the changed orientation of the shifted bats corresponds directly to the degree of the horizontal shift of the magnetic field. However, the unimodal Northwards orientation of the shifted bats represents a dramatic shift in behaviour from the control bats suggesting that the bats are able to sense the magnetic field shift. Furthermore, the random distribution of the inclination-reversed bats is a contrasting result to both the control and shifted bats. Significantly, these results provide the first evidence that the Earth's magnetic field is used for orientation by migratory bats, and specifically we have shown that sunset calibration is likely to involve the magnetic field.

The bimodality of the control bats has not been observed in previous studies of *P. pygmaeus*, but has in *P. nathusii* at the same location [8]. In late summer, the generally expected migratory direction of *P. pygmaeus* is south towards central Europe [8], however there is still little known about the migratory route of this bat species and it is possible that two migratory routes are used; one following the coast southwards, and another that goes northwards into Scandinavia and only then proceeds in a south westerly direction [15]. It is also possible that there is a mix of resident and migratory individuals at the field site, although if that were the case then we might not expect such a clear unimodal preference for North in the shifted bats. The response of the shifted bats does not fall in line with predictions according to the 120° shift, which would result in a 120° counter clockwise rotation of the compass once tested in the natural magnetic field, with an expected mean orientation of 60° for Southward-heading bats, and a mean orientation of 240° for Northward-heading bats. The orientation of the shifted bats may instead be due to a reversal of migratory orientation direction, which is frequently observed in migratory animals [16,17], and may be a stress response due to the unusual alignment of the magnetic field in respect to the location of the setting sun. Interestingly, the behaviour of the shifted bats suggests that the magnetic treatment had a unifying effect, reverting the preference of all bats to a common direction, in this case North; the opposite of the generally expected migratory direction.

It has been observed in a species of migratory bird that inclination reversal (without a horizontal shift) reversed their orientation [18,19]. If the effect of any magnetic manipulation were to reverse migratory direction, perhaps due to stress or confusion, then we would expect the same to be the case for the shifted-and-inclination-reversed treatment group. However, we found that the orientation of the inclination-reversed bats is not statistically distinguishable from random. This difference between the 120° shift and the shift 120° with reversed inclination is suggestive of the bats being able to detect differences in the horizontal and vertical components of the magnetic field, and therefore an ability to sense magnetic inclination. The combination of magnetic total intensity and inclination that the inclination-reversed bats experienced can naturally be found in the Southern Indian Ocean (see ESM2). If the altered declination resulting from the shift is also considered, then there are no possible locations where these magnetic parameters occur naturally. Therefore, whilst the shifted bats experienced only a rotated field, the shifted-and-inclination-reversed bats experienced a magnetic field very different from anything they would normally experience which may explain the lack of any directionality. To rule out the possibility that this effect may have been due to radio frequency (RF) noise artefacts produced by the coil setup[20], we tested our coil setup for RF noise but found no differences between treatments (see ESM4). A confused or stress response, therefore, would again appear to be the most likely explanation considering the lack of any significant orientation direction as would be predicted if an inclination compass were being used.

Significantly, the magnetic manipulations that we applied occurred only during the sunset period. Bats were later released in a natural magnetic field, with all other environmental cues obscured. The effects of the magnetic manipulations are therefore long-lasting, modifying bat behaviour hours after they were removed from the altered magnetic field conditions. This suggests either that the sunset period is key to calibrating a magnetic compass, or in the case that a magnetic compass is not being utilised, that regardless, magnetic fields are responsible for producing a long lasting behavioural reaction in migratory bats.

ETHICS STATEMENT

All work was conducted under the permit no. 21/2021 to the Institute of Biology, University of Latvia. All experimental procedures were conducted in accordance with national and local guidelines for the use of animals in research.

DATA ACCESSIBILITY

The data are provided in the electronic supplementary material.

COMPETING INTERESTS STATEMENT

We have no competing interest.

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